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THE FLORAL DEVELOPMENT AND EMBRYOGENY OF ERIOCAULON SEPTANGULARE

R. WILSON SMITH

(WITH PLATES XIX AND XX)

Flowers

The inflorescence of *Eriocaulon septangulare* is a compact head of staminate and pistillate flowers. The two kinds of flowers are sometimes intermingled, but the most common arrangement is in groups of 10–30, all the members of each group exhibiting nearly the same stage of development. During the season there are usually about three successive groups of each kind of flower.

Longitudinal sections of the flower show that the parts appear in acropetal succession. The two sepals, and likewise the two petals, arise from the floral axis at somewhat different levels. This is probably to be interpreted, not as the survival of a primitive spiral arrangement, but as a result of the intercalary growth which is a marked feature especially of the inner flowers (*fig. 5*). Rudimentary carpels surrounding the tips of the floral axis occupy the center of the staminate flower (*fig. 1*), but do not progress beyond the stage shown in the figure; they can still be recognized readily in the old flowers. In the pistillate flowers the stamens are represented by rudimentary outgrowths put out above the petals and having their extremities of withered and blackened cells (*fig. 2*). Each flower is subtended by a bract and bears large conspicuous nectaries upon the petals. Transverse sections are shown in *figs. 3* and *4*. *Fig. 3b* and corresponding sections of the pistillate flowers show that the stamens belong to one cycle, and hence the flowers are tetracyclic.

The manuals describe this and other species of Eriocaulon as having the parts of the flowers in twos and threes, but in and about Lake Joseph, Ontario, where this material was collected, I have been able to find only the former type of flowers. Do these constitute a local race, or will other localities furnish similar examples of the constancy of dimerous symmetry?

Stamens

The stamens bear four narrow sporangia, whose hypodermal cell walls show the usual thickening, but not prominently so, and whose cavities before dehiscence unite in pairs. The pollen mother cells of each sporangium are in a single row, surrounded completely by a tapetum, and externally by two or sometimes three cell layers (*fig. 6*). They are somewhat flattened lengthwise of the anther, and in conformity with this peculiarity of shape and arrangement they exhibit an interesting polarity, the spindles of both divisions standing at right angles to the long axis of the sporangium. Many of the stamens fail to mature their microspores. The ripe microspores contain a large vegetative nucleus and two male cells. In good sections the latter can be seen to have an elongated pointed outline, and to be distinctly delimited from the remaining cytoplasm by a plasma membrane (*fig. 7*). The exine possesses strong thickening bands studded with minute spines (*fig. 8*).

Ovule and embryo sac

The position of the ovules and their relation to the carpels are illustrated in *fig. 5*. It will be seen that they are distinctly axial. They point outward at first toward the carpels, but gradually bend downward so that finally the micropyle is directed toward the base of the flower. The archesporial cell remains undivided for a long time, lengthening with the enlarging ovule (*figs. 9, 10*). Finally, without cutting off any parietal cell it segments into four megaspores, the innermost of which becomes the embryo sac (*fig. 10*). In a large number of cases several or all of the megaspores germinate, both by increase of size and by division of their nuclei. While thus increasing in size, some of them accommodate themselves to the space in which they lie by slipping past one another so as to lie side by side. Many cases somewhat similar to *fig. 12* were observed; also in sections of the same age as *fig. 13* a group of five or six nuclei above the embryo sac, and no doubt consisting of the unabsorbed nuclei of the sterile megaspores, can frequently be seen. But while it is perhaps the rule for more than one megaspore to germinate, I have never found two fully formed embryo sacs in one ovule, nor other than the lowermost megaspore the successful competitor.

About this time or a little later the nucellar tissue lateral to the megaspores begins to be broken down and absorbed by the growing embryo sac. A few of the apical cells of the nucellus, however, persist for a long time, and enlarging assume the appearance of a "tapetum" (*figs. 12–14, n*). These too are ultimately absorbed, and then the embryo sac abuts directly upon the inner integument and micropyle.

The development of the embryo sac is quite normal, so that little explanation need be added to the figures. The central vacuole first appears at the four-nucleate stage. During the three successive divisions there is little if any increase of nuclear material; probably the eight nuclei of *fig. 16* have no greater aggregate volume than the single nucleus of the megaspore.

In the succeeding pre-fertilization organization of the embryo sac some of these nuclei become greatly enlarged (cf. *figs. 16* and *18*, which are drawn to the same magnification). A nearly mature embryo sac is shown in *fig.* 17. The antipodals are never conspicuous. After the inception of endosperm formation they become difficult of recognition, but occasionally may be seen in a small pocket below the endosperm. The upper polar nucleus moves down to meet the lower one near the antipodals. From the frequency with which they are found in contact with each other, it may be inferred that their fusion is very gradual. It is attended with considerable growth of the fusing nuclei, and there is still further growth subsequent to their fusion (cf. *figs. 17, 18, 22*). Probably this enlargement of the definitive nucleus is correlated with the rapid production of endosperm consequent on fertilization. There is much variation among plants as to the time when the polar nuclei fuse and the relation of this fusion to pollination and fertilization. Thus in Elodea WYLIE (**15**) found that the actual presence of the pollen tube in the embryo sac is necessary to bring about the fusion. In Eichhornia (SMITH **14**) the fusion occurs before pollination, and in Sagittaria (SCHAFFNER **13**) before the entrance of the pollen tube. Further examples are given in COULTER and CHAMBERLAIN'S *Morphology of angiosperms* (**6**, pp. 95, 96). There can be no doubt that in Eriocaulon the fusion is independent of the stimulus of pollination, for it was found complete in numerous heads taken from beneath the surface of the water. On the other hand, division of the endosperm nucleus does not appear to take place in the absence of fertilization.

Beneath the embryo sac there is a group of strongly thickened cells which probably function as conduction tissue. They stain deeply, and occasionally one of them proliferates into the embryo sac (*fig. 19*).

Fertilization

Fertilization was not observed in a sufficient number of cases to make possible a very definite description of the process. The observations indicate that the pollen tube entering the micropyle passes through one of the synergids or between them without destroying either. The contents of the undischarged tube shown in *fig. 20* could not be made out, but there can be no doubt that both of the male cells or their nuclei enter the embryo sac. Three or four cases similar to *fig. 22* were seen, and once I found a sperm nucleus (which had then lost its cytoplasmic sheath) about half-way between the egg and the definitive nucleus. Pollination and fertilization are apparently effected in the first flowers within the first day of their emergence from the water. The sexual nuclei in the egg fuse without delay, and their fusion is soon followed by that of the second sperm and the definitive nucleus.

Only one case of polyembryony was observed, the three embryos apparently originating from the two synergids and the egg (*fig. 34*).

Endosperm

The first division of the endosperm nucleus was not seen. The nuclei multiply rapidly, so that 16–32 of them are distributed about the periphery of the embryo sac before the first segmentation of the egg. They are elongated and flattened, and invariably take a position in the inner border of the parietal cytoplasm (*fig. 23*). When their number is about 64, tissue formation begins by the appearance of delicate walls across the cytoplasmic layer. The walls appear first in the micropylar and antipodal regions, and somewhat later about the sides of the embryo sac. At this time the inner boundary of the cytoplasmic layer has no definite wall (*fig. 24*), and the general appearance is similar to that figured and described by LAWSON (11) as occurring in the gametophyte of Cryptomeria;

but the analogy stops here. In Eriocaulon the endosperm cells are never binucleate and the first-formed walls are permanent.

The cells continue to extend centripetally by vacuolization, and then undergo periclinal division, resulting in an outer layer of flat cells which do not divide further, and an inner layer of larger cells (*fig. 25*). At this time no starch is present. The inner layer by further divisions obliterates the central cavity of the embryo sac and then rapidly fills with starch grains. In the ripe seed three regions of the endosperm are recognizable: (1) the outer layer, still more flattened and containing little starch; (2) the large thin-walled cells of the interior, with abundant starch; (3) a deeply staining group of starch-containing and elongated cells near the base.

Embryo

It is in the development of the embryo that this plant deviates more widely from ordinary angiosperms. The first division is, as usual, transverse (*fig. 27*). Each of the two resulting cells then divides in a longitudinal direction, the one toward the base of the sac dividing first as a rule (*figs. 28, 29*). The next divisions are also longitudinal, and at right angles to the preceding (*fig. 30*). Thus the embryo has no suspensor whatever, and passes through regular quadrant and octant stages. While these divisions are taking place, the embryo becomes globular in form and its cytoplasm beautifully vacuolated. The octant division is followed by the cutting off of a dermatogen. The process is not simultaneous in the two halves. Thus in *figs. 31* and *32* it will be seen that the micropylar half has divided most rapidly, while in *fig. 35* it is the basal half. The embryo of the ripe seed is shown in *fig. 36*. It is bell-shaped with flaring edges, and quite frequently the edges are upturned, owing to the pressure of the endosperm. There is no differentiation of the embryonic organs, nor any indication where these shall have their origin.

It is doubtful if a comparison of the early segmentation of the embryo is of value in determining relationship. There is too much variation within certain orders, and often the peculiarities are too manifestly adaptive. The nature of the endosperm and the embryonic organs is much more significant.

I have found no detailed study of plants nearly related to Eriocaulon. In other plants mature undifferentiated embryos have been reported within recent years in numerous instances; for example, in Aigenetia (KUSANO 10) and Peperomia (CAMPBELL 2); also Gunnera (MODILEWSKI 12) has no suspensor, and Piper (JOHNSON 8) but a slight one. But undoubtedly the nearest parallels to the embryo sac of Eriocaulon as yet described are among the Araceae and the Nymphaeaceae. Thus in Arisaema (GOW 7) the mature embryo sac is globular and without differentiation of organs; but its first three cells are in a row, and its early divisions are less regular. From CAMPBELL's studies of the Araceae (1, 3, 4) it appears that the globular form of the embryo is characteristic of that order. But the embryos figured by him show far more irregularity in their development than is the case in Eriocaulon. CAMPBELL regards the absence or slight development of the suspensor (as in Aglaonema 1 and Spathicarpa 3) as correlated with the complete investment of the embryo by endosperm tissue. In all the Araceae examined the endosperm was found to be septate from the beginning. The same is the case in Gunnera. It will be seen, however, that this explanation will not apply to the lack of a suspensor in Eriocaulon, since divisions of the embryo up to the octant stage precede tissue formation in the endosperm, and even for some time afterward the walls of the endosperm are too weak to exert much pressure. Pistia, another aroid, was investigated by HEGELMAIER (8) in 1874, and its embryo as described by him is in its early history practically identical with that of Eriocaulon. It shows the same regularity of form and sequence up to the cutting off of the "dermatogen-like outer layer," and for some time thereafter, except that for a time in individual cells of this layer periclinal divisions now and then occur, a phenomenon I have not observed in Eriocaulon. In the ripening seed of Pistia the globular embryo becomes indented, and root tip and cotyledon are developed.

Somewhat similar embryos occur in *Castalia odorata* and *Nymphaea advena* (COOK 5) and in Nelumbo (YORK 16). These are described as passing through quadrant and octant stages, less regular than those of Eriocaulon and Pistia. The case of Nymphaea is particularly interesting. Though the extent of the dermatogen is not stated, from the figures it appears to invest the embryo completely, and there is no trace of a suspensor. Later, however, after the position of the cotyledon is indicated, a short suspensor is developed through the activity of one of the basal cells.

Experiments are now in progress to ascertain what changes the embryo of Eriocaulon undergoes in germination.

Summary

1. Eriocaulon gives evidence of derivation from a bisporangiate ancestor in that the pistillate and staminate flowers possess rudimentary stamens and pistil respectively.
2. The flower is tetracyclic.
3. The ovules are placed laterally upon the axis.
4. Four megaspores are produced, the innermost of which is fertile, but the others in a large number of ovules begin germination.
5. The embryo sac develops in the usual way.
6. "Double fertilization" occurs.
7. The embryo has no suspensor; its first division wall is transverse; quadrant, octant, and periclinal divisions follow; and no embryonic organs are recognizable in the ripe seed.

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EXPLANATION OF PLATES XIX AND XX

All the figures were drawn with the aid of an Abbé camera and a Leitz microscope, and have been reduced one-half in reproduction. The reference letters are as follows: *b*, bract; *s*, sepal; *p*, petal; *a*, stamen; *c*, carpel; *t*, tapetum; *n*, apex of nucellus.

FIG. 1.—Longitudinal section of staminate flower. ×105.

FIG. 2.—Longitudinal section of pistillate flower. ×105.

FIG. 3*a*.—Transverse section of staminate flower. ×105.

FIG. 3*b*.—Transverse section of same flower at the level of the origin of the stamens; *p*, petals and gland. ×105.

FIG. 4.—Transverse section of pistillate flower. ×105.

FIG. 5.—Superficial view of pistillate flower with bract (*b*), sepals (*s*), and petals (*p*) removed; ovules and apex of flower axis seen through the ovary wall. ×80.

FIG. 6*a*.—Transverse section of a microsporangium at the mother cell stage. ×730.

FIG. 6*b*.—Part of longitudinal section of microsporangium of same age as the preceding. ×730.

FIG. 7.—Section of mature microspore. ×730.

FIG. 8.—Surface view of mature microspore. ×730.

FIG. 9.—Longitudinal section of ovary with archesporium. ×730.

FIG. 10.—Same at older stage. ×730.

FIG. 11.—The four megaspores. ×730.

FIG. 12.—Germination of megaspores. ×730.

FIGS. 13–17.—Successive stages in development of embryo sac. ×730.

FIG. 18.—Definitive nucleus before fertilization. ×730.

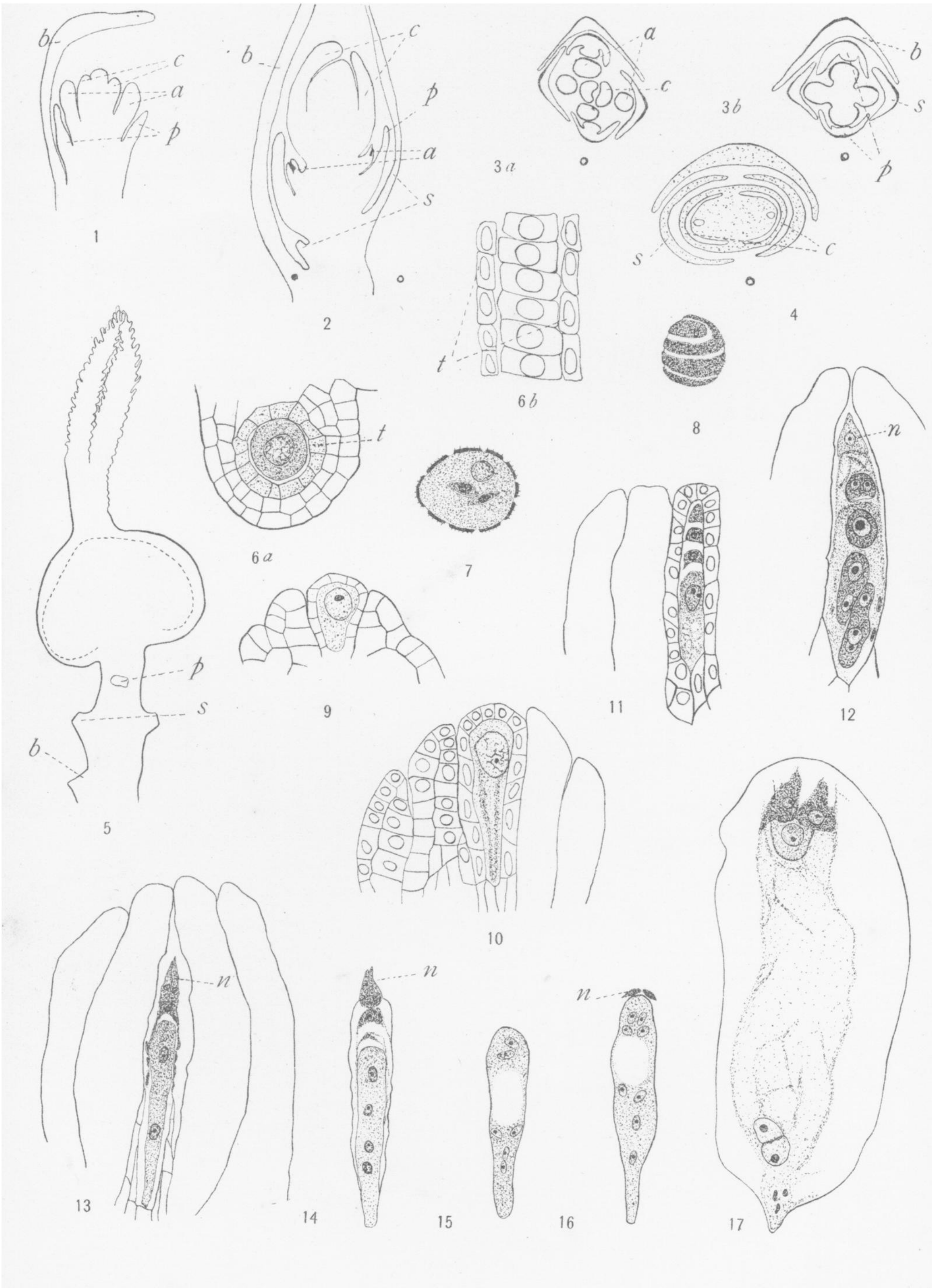
FIG. 19.—Proliferation into the base of the embryo sac. ×730.

FIG. 20.—Egg apparatus and entrance of pollen tube. ×730.

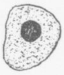
FIG. 21.—Egg apparatus after fertilization. ×730.

FIG. 22.—Fusion of second male nucleus with definitive nucleus. ×730.

PLATE XIX



SMITH on ERIOCAULON



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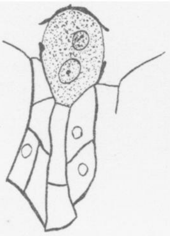

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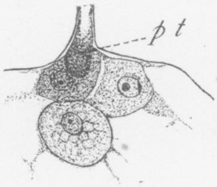

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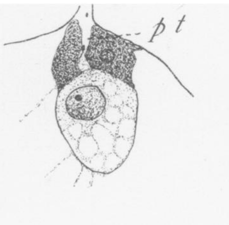

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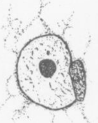

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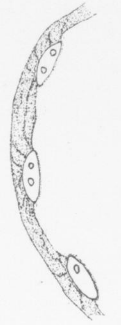

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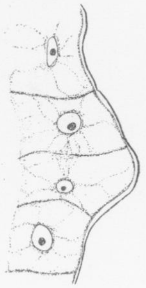

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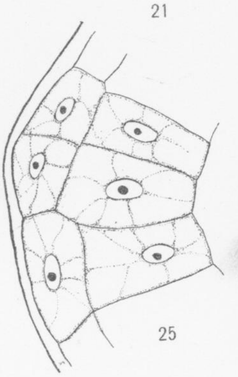

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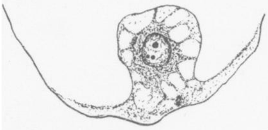

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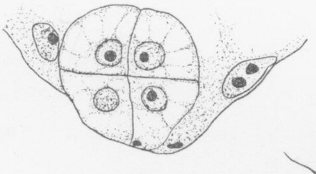

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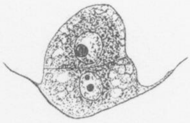

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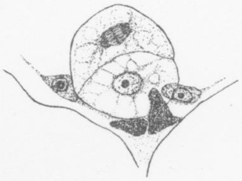

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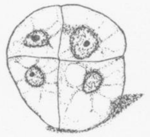

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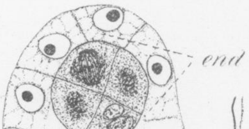

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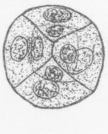

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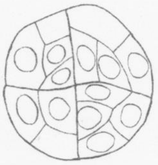

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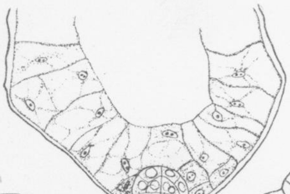

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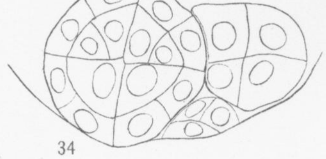

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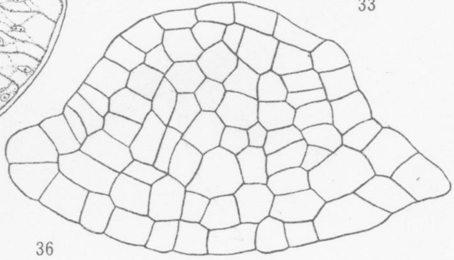

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SMITH on ERIOCAULON

FIG. 23.—Endosperm before tissue formation. ×730.

FIG. 24.—Tissue formation in endosperm. ×490.

FIG. 25.—Division of parietal layer of endosperm. ×730.

FIG. 26.—One-celled embryo. ×730.

FIG. 27.—Two-celled embryo. ×730.

FIG. 28.—Second division of embryo. ×730.

FIG. 29.—Quadrant stage of embryo. ×730.

FIG. 30.—Octant stage of embryo. ×730.

FIG. 31.—Transverse section of inner half of embryo, showing origin of dermatogen. ×730.

FIG. 32.—Transverse section of micropylar half of same embryo. ×730.

FIG. 33.—Transverse section of an older embryo. ×730.

FIG. 34.—Polyembryony.

FIG. 35.—Micropylar end of embryo sac, showing embryo and endosperm. ×240.

FIG. 36. Longitudinal section of embryo of mature seed. ×730.